

ORIGINS AND DISPERSAL OF A BRACHIOPOD FAMILY—THE SYSTEMATICS, BIOGEOGRAPHY AND EVOLUTION OF THE FAMILY TEREBRATELLIDAE

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Three southern subfamilies of the Terebratellidae (Bouchardiinae, Anakineticinae, Terebratellinae) are redefined using cardinal process shape and presence or absence of some components of the cardinalia (crural bases, hinge plates). The subfamilies are confined to the seas around Gondwana-derived land masses between Antarctic shorelines and latitudes of approximately 30°S and, with the exception of 2 Late Cretaceous genera, to the Cainozoic era. Species without adaptations for particular substrates in Antarctica, the subantarctic islands, Australia, New Zealand and South America show certain similarities suggesting that they were derived by vicariance from generalist stocks which occupied some sections of the shorelines and shelf of Gondwana. This record of the Terebratellidae does not conform with the only current model for brachiopod distribution (Zezina 1985)—that seas in low latitudes have provided both a cradle and refuge for inarticulates and articulates.

THE PHYLUM Brachiopoda provides a record of life on earth that is remarkable in the history of its 2 divisions, one of which (Inarticulata) is static, the other (Articulata) repetitive (Cooper 1970; Rudwick 1970). Despite the excellence (in length, continuity and abundance) and clarity of the record, studies have yielded little information on the processes of macroevolution or on the nature of relationships within the phylum. Difficulties in utilising the record can be attributed in large part to the lack of knowledge of the variability of living populations and so of the nature of relationships between species—one consequence of the inaccessibility of living species in many parts of the world. For example, New Zealand is the only country known in which species of polytypic genera are known to be accessible to direct study.

During the last 2 decades studies of the members of one family, the Terebratellidae, have given greater biological understanding of articulate brachiopods. This family provides more information than others because it is the only one in which living outnumber fossil genera and because of the abundance of its members in the Southern Hemisphere. In the Ross Sea, for example, Foster (1974, 1989) has observed that brachiopods outnumber bivalve molluscs. They are common to abundant in the Magellanic province of South America (McCammon 1973; Cooper 1973), the subantarctic waters of the Atlantic (Cooper 1982) and Indian (Cooper 1981) oceans and in the sands of the shelf of southern Australia (Richardson 1987). In New Zealand they are dominant members of the benthos of many southern inlets and of all the fiords (Richardson 1981a).

The abundance of living members of the family in these areas has provided information on the variability of populations in most parts of its range and on factors that govern distribution. In addition many species are sufficiently accessible for the direct study of substrate relationships and behaviour. These studies of the living together with the rich Tertiary faunas of Australia and New Zealand mean that sufficient data are now available about the members of one family to enable speculation on the centres of origin of species, on paths and rates of dispersal, and on relationships among genera.

SYSTEMATICS

Superfamily Terebratelloidea King, 1850

Family Terebratellidae King, 1850

Diagnosis. Non-strophic Terebratellacea without spicules and dental plates and in which lateral connecting bands are formed during development of the loop. Upper Cretaceous to Recent.

Subfamily Bouchardiinae Allan 1940

Diagnosis. Sulcate, posteriorly thickened smooth Terebratellidae with a hypothyril or epithyril foramen, and with cardinalia consisting of socket ridges and a cardinal process with a bilobed posterior surface.

Genera included. *Bouchardia* Davidson, 1850; *Bouchardiella* Doello-Jurado, 1922; *Malleia* Thomson, 1927; *Neobouchardia* Thomson, 1927.

Distribution. Cretaceous–Recent; Australia, New Zealand, Antarctica, South America.

Subfamily Anakineticinae Richardson 1991

Diagnosis. Rectimarginate to sulcate, posteriorly thickened, smooth Terebratellidae with permesothyrid foramen, cardinalia consisting of socket ridges, crural bases and a cardinal process with trifid posterior surface.

Genera included. *Anakinetica* Richardson, 1987; *Adnatida* Richardson, 1991; *Aliquantula* Richardson, 1991; *Australiarcula* Elliott, 1959; *Elderra* Richardson, 1991; *Magadina* Thomson, 1915; *Magadinella* Thomson, 1915; *Parakinetica* Richardson, 1987; *Pilkenia* Richardson, 1991; *Pirotthyris* Thomson, 1927; *Rhizothyris* Thomson, 1915.

Distribution. Cretaceous–Recent; Australia, New Zealand.

Subfamily Terebratellinae King 1850

Diagnosis. Rectimarginate to sulcate to intraplicate, smooth or costate Terebratellidae with cardinalia consisting of socket ridges, crural bases, hinge plates and a transverse cardinal process, posterior thickening present or absent.

Genera included. *Aerothyris* Allan, 1939; *Aneboconcha* Cooper, 1973; *Austrothyris* Allan, 1939; *Calloria* Cooper & Lee 1993; Allan, 1939; *Diedrothyris* Richardson, 1980; *Dyscritosia* Cooper, 1982; *Fosteria* Zuzina, 1980; *Gyrothyris* Thomson, 1918; *Jaffaia* Thomson, 1927; *Magasella* Dall, 1870; *Magella* Thomson, 1915; *Magellania* Bayle, 1880; *Neothyris* Douvillé, 1879; *Pachymagas* Ihering, 1903; *Stethothyris* Thomson, 1918; *Syntomaria* Cooper, 1982; *Terebratella* d'Orbigny, 1846; *Vicrorthyris* Allan 1940; *Waiparia* Thomson 1920.

Distribution. Upper Cretaceous–Recent. Southern Hemisphere between Antarctic shelf and latitudes of approximately 35°.

Comments. Foster (1974), in a comprehensive study of Recent terebratellid species from the Southern Hemisphere, differentiated genera within the Terebratellidae on loop form. He stated that use of the loop seemed artificial but that it was the simplest means of classification in such a large group with 'the limited number of morphological features of apparent taxonomic value, the high degree of variability within individual species, the great amount of apparent convergence, and the poorly known fossil record' (1974, p. 97).

Work on Australian Tertiary Terebratellidae (Richardson 1973, 1980, 1991) has clarified relationships within the family to some extent in that three of the subfamilies (Bouchardiinae, Anakineticinae, Terebratellinae) can now be defined with greater precision using components that make up the cardinalia. The subfamily Neothyrinae is not retained because both Foster (1974) and Richardson (1975, 1980) have shown that the characters used by Allan (1940) to distinguish members of the subfamily (bifurcated septum and a hinge trough) are a consequence of the differential thickening of inner hinge plates; i.e. the Neothyrinae was erected for genera that differ from those included in the Terebratellinae only in degrees of calcification (Figs 1, 2).

The other subfamily (Trigonoseminae) referred to the Terebratellidae by Elliott (1965) includes three genera from Upper Cretaceous deposits in Europe, North America and Western Asia. Loop characters indicate that it should be assigned to the Terebratellidae but the nature of its relationship to southern subfamilies is difficult to determine without study of the cardinalia of juvenile specimens. Descriptions of the genera included in the

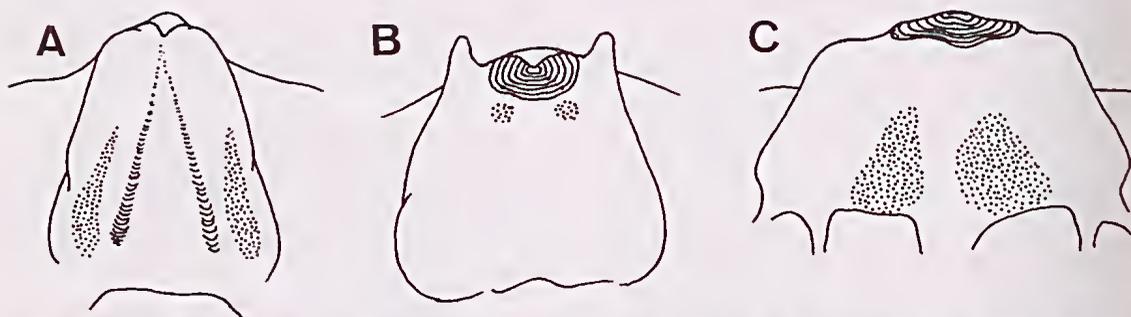


Fig. 1. Outline drawings of the cardinalia to show areas of attachment of the diductor and dorsal adjustor muscles in representative adults of the 3 terebratellid subfamilies—Bouchardiinae (*Bouchardia rosea*), Anakineticinae (*Anakinetica cumingi*), Terebratellinae (*Magasella sanguinea*).

Trigonoseminae indicate that, like the Anakineticinae and free-living Bouchardiinae, the cardinalia are thickened and without hinge plates but otherwise they do not resemble any southern taxa. Furthermore, neither cardinalia nor the cardinal process appear to be consistent in form within the subfamily.

In the classification proposed herein, precedence is given to those characters associated with the substrate relationships of a species for 3 reasons:

1. Variability of the pedicle system. The pedicle system may vary intra- and interspecifically and within and between all higher taxa (Richardson 1981) whereas other soft parts (gut form, numbers of coelomoducts) may differ between orders but appear to be consistent in form and function in the members of each order.

2. Functional morphology. Features of the shell used in classification are directly related to differences in the pedicle system and therefore to substrate relationships. They are:

the beak and cardinalia that house and therefore reflect any differences in the pedicle system, e.g. the area of attachment of the dorsal adjustor muscles differentiates forms with a free or bonded pedicle (Figs 1, 2, 3);

the size of the cardinal process which is determined by the area of attachment required by the diductor muscles. The size of the process in free forms indicates that greater leverage is needed to open the shell in free than in fixed forms; and

differential thickening which is found in free forms only and is the means by which the shell is stabilised and oriented.

3. Species of polytypic genera and populations of species studied show that they are differentiated on characters reflecting differences in substrate relationships, e.g. the free and sedentary populations of *Calloria inconspicua* and of *Magasella sanguinea* (Aldridge 1981; Stewart 1981) and species of *Neothyris* (Aldridge 1991).

Some families of the Terebratellidae (Laqueidae, Dallinidae, Terebratellidae) are differentiated on the nature of loop development but the stage of development does not define lower categories. Adult loop patterns within a family appear to be correlated with the amount of space available within the mantle cavity since no species with a large mantle cavity is known with an axial loop and no species with a small mantle cavity is known with a teliform loop. From studies of Mesozoic Terebratelloidea, Owen (1977) has also stressed the importance of the cardinalia in defining taxa at subfamily levels.

The cardinalia and classification. Figs 1–3 illus-

trate differences in the cardinalia that distinguish the 3 southern subfamilies. They differ in cardinal process shape (bilobed, trifold, transverse), in the presence or absence of hinge plates and in the areas used for the attachment of the dorsal adjustor muscles. In the Terebratellinae these muscles are attached anterior to the cardinal process and to hinge plates which occupy the area bounded by the socket ridges. In the Anakineticinae and Bouchardiinae the muscles are attached to respectively pits and furrows that flank the cardinal process. The pits of the Anakineticinae are confined to the posterior part of the platform, the furrows of the Bouchardiinae extend the length of the platform. Differences in function associated with the position of attachment of the muscles are described under substrate relationships. The absence of crural bases in the Bouchardiinae is linked to the absence of descending branches of the loop which consists of a ring supported by a high median septum.

The hinge plates that characterise the Terebratellinae occupy the area bounded by the socket ridges. Hinge plates also differentiate genera within the subfamily according to their relationship with crural bases, socket ridges, median septum, and whether they are lamellar or solid, excavate or sessile i.e., adpressed to the valve floor.

The common pattern of the cardinalia in living terebratellinids is one in which the socket ridges and crural bases are fused or confluent or are narrowly separated by outer hinge plates with inner hinge plates meeting on the septum. In these species the crural bases are traces of the crura. In two Recent species, *Magellania joubini* and *Magellania fragilis*, the crural bases separate inner and outer hinge plates which are roughly equal in width. In this character, the hinge plates are similar to those in the Tertiary genera, *Diedrothyris* and *Stethothyris*. The crural bases of *Austrothyris* and *Cudmorella* (Fig. 3C) differ from those of all other genera in that they are prominent structures with sharp ridges which, in ventral view, project above the level of the hinge plates. In these genera also the inner hinge plates are adpressed to the valve floor and extend onto the median septum for approximately half its length. Foster (1974) has noted that the hinge plates of *Aerothyris kerguelensis* vary in position, most are sessile, others are excavate. The significance of differences in the position and prominence of crural bases and in the angle at which hinge plates lie relative to the valve floor and septum is unknown. Richardson & Mineur (1981) compared the hinge plates of *Magasella sanguinea* with those of *Calloria inconspicua* and concluded that the greater elevation of

the plates of the former species was related directly to the line of action of the dorsal adjustor muscles and indirectly to shell curvature and to beak and pedicle size. Analyses of hinge plate condition in relation to the functioning of the dorsal adjustor muscles in other species would be a productive study.

The cardinal process of the Bouchardiinae is bilobed with the posterior striated surface extending as an inverted V from the posterior tip of the dorsal valve. Differences in the extent of the lobes in different genera are presumably associated with life style. *Bouchardia* is a free living form with a free pedicle which probably functions in similar

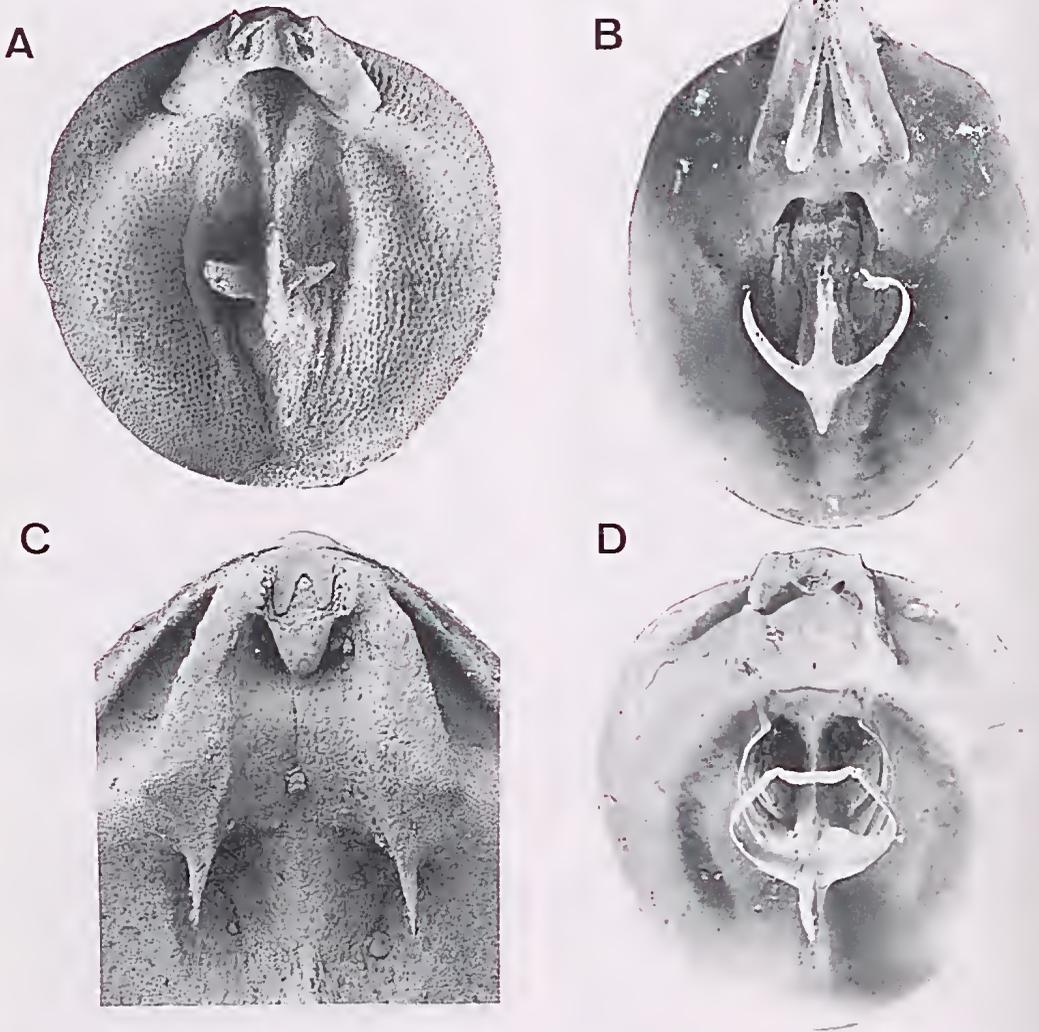


Fig. 2. Dorsal valve interiors of species from the subfamilies Bouchardiinae and Anakineticinae which show differences in the cardinal process and in the areas used for attachment of the dorsal adjustor muscles. A, B, *Malleia portlandica* ($\times 12$) and *Bouchardia rosea* ($\times 5$) (Bouchardiinae) with bilobed cardinal processes and with areas of attachment of the dorsal adjustor muscles lying between the socket ridges and the cardinal process. C, D, *Anakinetica cumingi* (Anakineticinae), young ($\times 30$) and adult ($\times 5$) specimens with trifid cardinal processes and attachment for the dorsal adjustor muscles at the antero-lateral corners of the posterior surface of the cardinal process.

ratechet-like fashion to that of *Anakinetica*. *Malleia* (Tertiary) was probably sedentary in habit in that its small size and back, plano-convex shape and hypothyrid foramen are features associated with fixed forms in modern seas.

The striated posterior surface of the cardinal process of the Anakineticinae is trifid, i.e. it con-

sists of three surfaces approximately equal in size, two lateral surfaces flanking one ventrally facing median surface.

The cardinal process of most of the species included in the Terebratellinae is transverse with a median notch at the junction of the striated posterior and smooth anterior surfaces. The car-

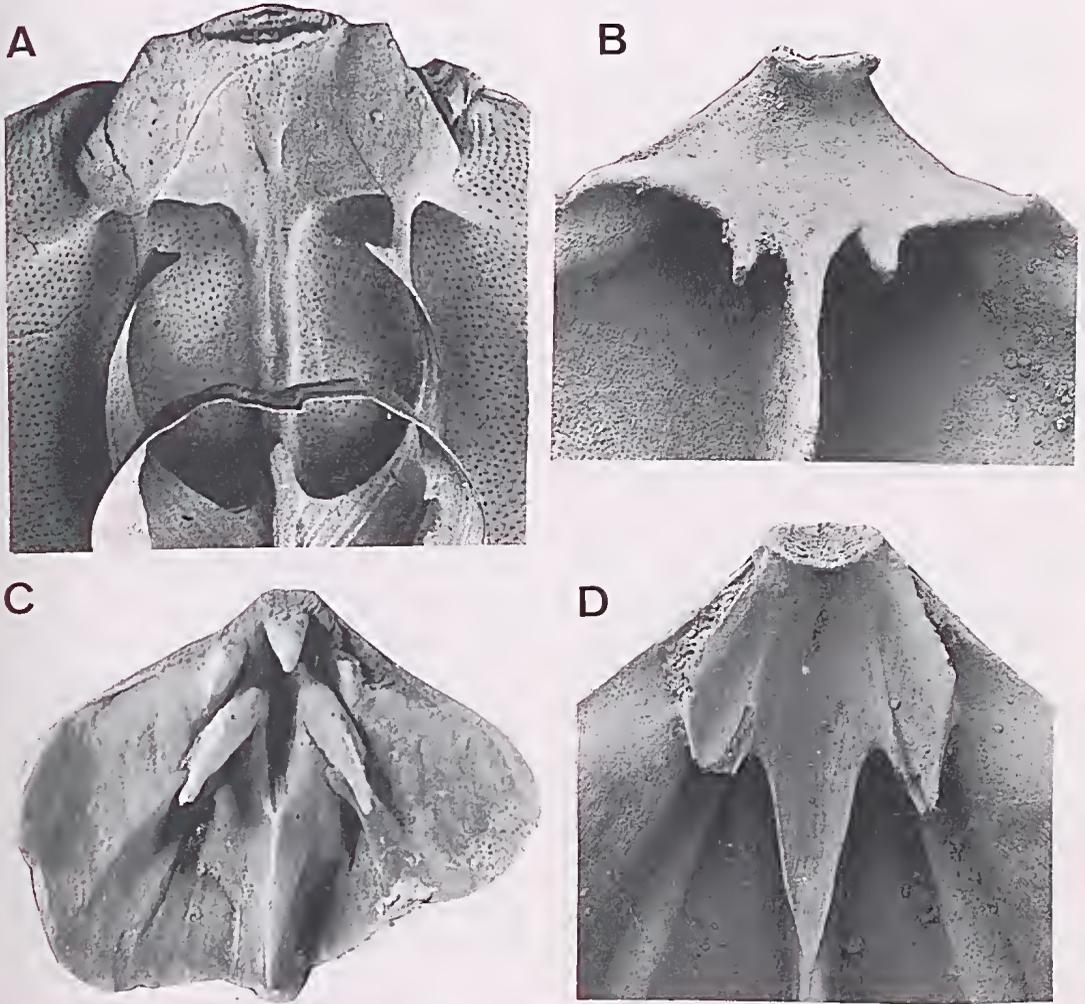


Fig. 3. Dorsal valve interiors of species of terebratellinae genera which illustrate cardinal process shape (transverse), differences in the disposition of hinge plates which provide areas of attachment of the dorsal adjustor muscles, and the effects of differential thickening on the appearance of the cardinalia. A, *Neothyris lenticularis* juvenile ($\times 30$). B, *Stethothyris pectoralis* ($\times 6$) juvenile in which erural bases separate inner and outer hinge plates. C, *Cudmorella corioensis* ($\times 3$) juvenile in which erural bases with sharp ridges project above the level of the hinge plates and in which inner hinge plates extend anteriorly onto the septum. D, *Cudmorella corioensis* adult ($\times 1.5$) in which differential thickening gives a superficial appearance of bifurcation of the septum.

dinal processes of young specimens of *Anakinetica cunningi* and *Neothyris lenticularis* (Figs 2C, 3A) show the differences in shape characteristics of the two subfamilies. In terebratelline species with differential thickening, the anterior surface of the cardinal process is large and may be globose or columnar in outline. *Neothyris lenticularis*, in particular, shows great variability in the shape of the process and, as noted by Foster (1974), specimens may display lateral flanges with strong inwards curvature and a trefoil posterior surface. Similar convergent trends have been described by Cooper for the Productacea 'Each of the major families of the Productacea has its own type of cardinal process, characteristic of the family as shown by young or young adults but in old age all tend toward a common trilobed cardinal process' (1969, p. 229).

Morphological variability. The genera included in the Bouchardiinae and Anakineticinae can be clearly defined but the variability of species within the Terebratellinae make generic separation difficult as noted by Foster (1974, 1989) and by Cooper from his studies of species from the subantarctic waters of the Atlantic (1982) and Indian (1981) oceans.

The genera included in the Terebratellinae are similar in folding, sulcate to intraplicate; foramen position lies within the range submesothyrid-mesothyrid-permesothyrid; the loop is either free or with transverse bands connecting the descending branches and the septum; the shell may be smooth, partially or fully ribbed. The only consistent associations of characters appear to be foramen type with shell thickness, a submesothyrid foramen with an unthickened shell and a permesothyrid foramen with a thickened shell (thick shells however are not necessarily permesothyrid). The shells of species with a mesothyrid foramen may be differentially thickened (*Neothyris*, all species), unthickened (*Magellania flavescens*, *M. fragilis*, *M. joubini*) or variable in thickening (*Magellania macquariensis*, *M. kerguelensis*, *M. venosa*, *Terebratella dorsata*).

The difficulties in separating terebratelline lineages is well illustrated by those species which have been attributed to *Magellania* by Foster (1974, 1989). Cooper (1981) considers that the species *macquariensis* and *kerguelensis* should be placed in *Aerothyris* and Zezina (1985) has placed *spinosa* in her new monotypic genus *Fosteria*. (Foster, in 1974, had described the species as very similar to *M. fragilis* and *M. joubini* except in the possession of spinose descending branches. Spinosity occurs to a varying extent in the loop development of

many species and, since members of the species are small, separation on this one morphological feature may not be justifiable.) There seems little doubt, as recommended by Cooper (1981) that *M. flavescens* (the type species) and *M. venosa* should be in different genera and it would be desirable if a worker with access to good collections of *Magellania venosa* would take this step. Foster (1989) states that a better understanding of this species is essential in order to evaluate the number of similar species that occur in the same area and which may be variants of *M. venosa*. They include species of *Aneboconcha*, *Syntomaria* and *Dyscritosia*. Until such a study can be undertaken, morphological and distributional patterns suggest that the most natural grouping of these species would be as follows:

1. *Magellania flavescens*.
2. *Aerothyris macquariensis* and *A. kerguelensis*.
3. *Magellania venosa*, *M. joubini*, *M. fragilis*, *Fosteria spinosa*, *Aneboconcha obscura*, *Dyscritosia secreta*, *Syntomaria curiosa*.

Magellania flavescens is distinguished from all other species by beak characters (long with deltidial plates invariably fused with a round mesothyrid foramen) and ornament. Species of *Aerothyris* are smooth with a short beak, a keyhole mesothyrid foramen and short deltidial plates which are commonly but not invariably disjunct. The third group includes smooth forms with a short beak, submesothyrid to mesothyrid foramina and deltidial plates that are short and commonly conjunct in species that are moderate to large in size (*Magellania venosa*, *M. joubini*, *M. fragilis*) and rudimentary in species that are small in size (*Fosteria spinosa*, *Aneboconcha smithii*, *A. obscura*, *Syntomaria curiosa*, *Dyscritosia secreta*). *Pirothyris* was included in the Anakineticinae (Richardson 1991) on the form of the cardinal process although earlier studies on the development of *P. vercoi* (Richardson 1975) had shown that inner hinge plates form and thicken early in ontogeny. *Pirothyris* is an atypical terebratellid with links to the Terebratuloidea in shell shape (depth greater than width) and folding (uniplicate) and cases could be made for including it in either the Anakineticinae or the Terebratellinae.

SUBSTRATE RELATIONSHIPS

Knowledge of the substrate relationships of species is of the greatest importance in any family study firstly because distribution is governed by the capacities of different species to colonise substrates, secondly because of the strength of the correlation between substrate type, morphology

and life style. The strength of this association in articulate brachiopods is evident in the numerous instances of homeomorphy they provide.

All terebratellid species are pediculate but they differ in relationships with the substrate and these differences are evident in the variability of the pedicle and of its housing—the beak and cardinalia. Some species are generalist in character and occupy an apparently unlimited range of substrates, others are highly specialised forms which function only in a particular type of sediment.

Species defined as generalist have the capacity to settle and survive on substrates of any size. In these species the pedicle functions as a pivot when bonded with large substrates and as a moving part when bonded with small (Richardson 1986). Therefore life style varies according to the size of the substrate used for settlement, bondage with a large substrate such as a rock face resulting in a sedentary life style, bondage with a small (relative to shell size) substrate in free life on the sea floor. The movement of either the shell or the pedicle (with its bonded substrate) prevents the build-up of sediment on the shell surface. The phrase 'bonded substrate' is used in preference to 'attached substrate' because of the confusion associated with the latter. The word 'attach' has been used to describe the union between the pedicle and substrate and also as an adjective synonymous with pediculate and sedentary, i.e. an attached brachiopod. Many adult articulates retain the larval substrate but live as free forms on soft sediments and would therefore be described as both permanently attached and free. Thus, 'attach' and all its derivatives perpetuate the falsity of the assumption that articulate brachiopods are uniform in life style and that free brachiopods are 'fallen' forms.

The generalist species most extensively studied *in situ* is *Magasella sanguinea* (Richardson 1981a, 1981b; Foster 1989). It is a common inhabitant of shallow subtidal waters in New Zealand, both on rock faces (sedentary individuals) and the sea floor (free individuals) where it is as common in mud as in coarser sediments. Free individuals are found lying on either valve. The shell is invariably unthickened, biconvex, the beak short with a large submesothyrid to mesothyrid foramen. It is highly variable in shape and size and, in these and other attributes, closely resembles *Terebratalia transversa* (Schumann 1991) and *T. coreanica* (Richardson et al. 1989), examples of generalist species from the Laqueidae and which occupy eastern and western shorelines of the northern Pacific Ocean.

Generalists are found in areas in which sites for settlement show a wide variation in size; i.e. they occupy shoreline areas or shelf sediments in

which the components vary in size; e.g. the till of Antarctic shelves. They may also be retrieved, although not in large numbers, from shelf sediments of more uniform grain size. For example, the distribution of *Magellania flavescens* on shelf sediments has been studied in southern Australia where the middle and outer shelf is covered with bryozoan sands. *M. flavescens* has been dredged from this area together with forms specialised for this particular sediment (Richardson 1987). However, collections by scuba in this high energy environment show that *M. flavescens* occurs only as a sedentary form, individuals being bonded to the scattered reefs and outcrops that occur on the shelf. Specimens from these areas are smaller and squatter than individuals from shoreline habitats.

Of the living terebratellid species studied none, like the micromorphic members of the Kraussinidae, Megathyrididae and Platidiidae are exclusively sedentary in habit. All members of the Bouehardiinae and Anakineticinae are free forms specialised for life in bryozoan sands. Members of the Terebratellinae are more varied morphologically and less specialised in life style. Two genera, *Neothyris* and *Gyrothyris*, are free forms which do not appear to be specific to a particular sediment, they are invariably thickened with a mesothyrid foramen and a variably curved beak. The remaining taxa are generalist to the extent that they appear to live as either free or sedentary individuals but shape, size range, pattern of distribution all indicate tendencies towards one or other life style. For example, *Magasella sanguinea* is as common on soft sea floors as it is on hard substrates, whereas species of *Calloria* are more commonly found (Stewart 1981; Doherty 1979) on rocky substrates. Stewart has shown that differences in the habitats of populations of *C. inconspicua* are also evident in the mean size and shape of individuals.

All other terebratellid taxa are known from dredged material only. Species of *Aerothyris*, *Magellania venosa*, *Terebratella dorsata* are all variably thickened which would suggest that they occur predominately, if not exclusively, on soft sediments. They are not as specialised for free life as species of *Neothyris* and *Gyrothyris* in which shell thickening is of early inception and invariably present. Unthickened dredged forms (*Syntomaria*, *Aneboconcha*, *Dyscritosia*) occur in the size range recorded for *Calloria*. They were collected (Cooper 1982) from the vicinity of islands in the South Atlantic and Foster (1989) considers that they may represent young populations of *Magellania venosa*.

Differences in the capacity for colonisation are important to note in any studies of dispersal. Since

generalists have the capacity to colonise substrates of any type they are also less affected by environmental events that cause changes in substrates. Specialists can colonise only those substrates that they are morphologically adapted to occupy. The patterns of settlement and survival in one area illustrate the latter point. New Zealand's Paterson Inlet contains 4 species all of which settle at random on surfaces of any size and composition (Richardson 1981a). Only the generalists (*Magasella sanguinea* and *Calloria inconspicua*) survive as adults on larval substrates of any size, one species (*Notosaria nigricans*) is restricted to large substrates, the other (*Neothyris lenticularis*) to small.

DISTRIBUTION

With the exception of the Trigonoseminae, the subfamilies of the Terebratulidae are confined to the Southern Hemisphere between Antarctic shorelines and latitudes of approximately 30°S and, with the exception of 2 genera, to the Cainozoic era. The subfamilies Bouchardiinae and Anakineticinae contain a larger number of fossil than living genera while the Terebratulinae contains more living than fossil. The earliest fossil genera of the Bouchardiinae (*Bouchardiella*) and the Anakineticinae (*Australiarcula*) occur in the Cretaceous while the Australian Eocene genus *Diedrothyris* is the oldest terebratuline known. Living Bouchardiinae occur only in Brazil, Anakineticinae in Australia while the Terebratulinae occur around the coasts and on the shelves of all land masses found between the Antarctic and latitudes of 35°S.

Foster (1974) showed that members of the Terebratulinae exist in very large numbers in the Southern Hemisphere in areas shallower than 1000 m and noted that *Magellania fragilis* and *M. joubini* are the most prominent species on the entire antarctic shelf. The map of distribution (Fig. 4) of the Terebratulinae is derived from Foster's figure (1974, p. 31) and has been extended to include the Australian species *Magellania flavescens* and Cooper's genera *Dyscritosia*, *Aneboconcha*, *Syntomaria* and *Calloria*.

The bathymetric range at which many species are found may be correlated with shelf depth. For example, the Ross Sea shelf is wide and deep (100 to 1000 m) and species occur at all depths. The New Zealand shelf and neighbouring rises (Chatham Rise, Campbell Plateau) rarely exceed depths of 400 m. *Magellania venosa* is most common at shelf depths approximately 300 m) but has been recorded from 5 to 1900 m and is the only terebratuline species known from the

slope. *Terebratella dorsata* commonly occurs with *Magellania venosa* on the shelf but has not been recorded from the slope.

All terebratuline species appear to live on varied shelf substrates and *in situ* observations in Australian and New Zealand waters show that they may be occupied by free (*Neothyris*, *Gyrothyris*) or free and/or sedentary forms (*Magellania flavescens*, *Magasella sanguinea*, *Calloria inconspicua*). The sites from which *Aerothyris kerguelensis* has been collected are recorded (Cooper 1981) as gravels, coarse and fine sands and muds. The greater part of the Ross Sea shelf is covered with till—unsorted material ranging from rock flour to boulders.

Fossil members of the Bouchardiinae and Anakineticinae occupy the same type of sediment in the same geographical areas as living members. *Bouchardia rosea*, the only living species of the Bouchardiinae, occurs in bryozoan sands off Brazil (Tommasi 1970). Mancenido & Griffin (1988) note that records of the genus range from Palaeogene (palaeolatitudes of 75°S to Neogene of 45°S) and that the present position of the genus at 35°S indicates displacement in a northward direction along the eastern margin of South America. The distribution of one member of the Bouchardiinae, *Neobouchardia minima*, is significant—it has not been recorded from modern seas but conspecific populations occur in the Oligocene–Pliocene of both New Zealand and Australia (Richardson 1973).

Living anakineticinids are found only in the bryozoan sands of the southern Australian shelf and these communities replicate those found in Australian Eocene–Pliocene calcarenites (Richardson 1991). New Zealand Oligocene deposits contain numerous species of each of 2 anakineticinid genera, *Magadina* and *Rhizothyris*, none of which have survived the reduction of shallow marine shelf environments during regressive phases in the Miocene. Like the Australian anakineticinid genera they were forms that were specific to carbonate sands.

New Zealand is the most valuable source of information on the distribution of living and fossil Terebratulinae. In the first place, all those genera with living species also occur in Tertiary deposits, secondly, abundant fossil deposits (shelly limestones) contain aggregates of species that replicate the brachiopod assemblages found in habitats on modern rocky shorelines (Richardson 1984). Similar deposits are rare components of the fossil record in other parts of the world. Two groups of genera can be distinguished in the New Zealand record. The first consists of extinct genera (*Waiparia*, *Stethothyris*, *Pachymagas*) all of which

show the morphological characteristics of forms specialised for a free life and which are known only from the Late Oligocene to Middle Miocene. The second group consists of genera with both living

and Tertiary species (*Magasella*, *Calloria*) which are common at or near modern rocky shorelines and in Eocene and Oligocene shelly limestones (Allan 1960; Richardson 1984). Species of *Neo-*

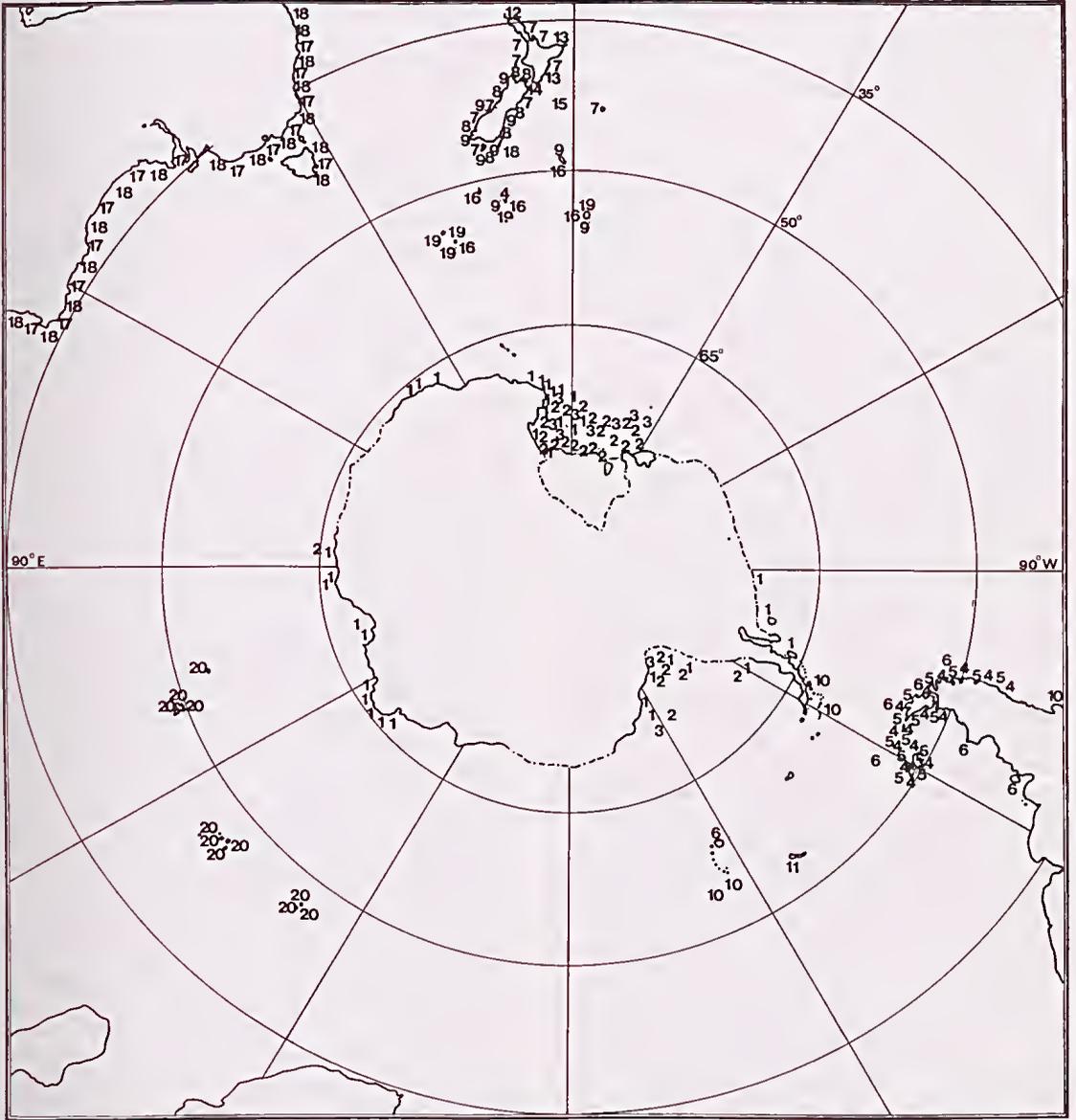


Fig. 4. Distribution of the species of the subfamily Terebratellinae from the records of Cooper (1973, 1981, 1982), Cooper & Doherty (1993), Foster (1974, 1989), McCammon (1973), Richardson (1981a, 1987). 1, *Magellania joubini*; 2, *Magellania fragilis*; 3, *Fosteria spinosa*; 4, *Terebratella dorsata*; 5, *Magellania venosa*; 6, *Aneboconcha obscura*; 7, *Calloria inconspicua*; 8, *Magasella sanguinea*; 9, *Neothyris lenticularis*; 10, *Syntomaria curiosa*; 11, *Dyscritosia secreta*; 12, *Calloria variegata*; 13, *Magasella haurakieusis*; 14, *Neothyris compressa*; 15, *Neothyris dawsoni*; 16, *Gyrothyris mawsoni*; 17, *Magellania flavescens*; 18, *Jaffua jaffaensis*; 19, *Aerothyris macquariensis*; 20, *Aerothyris kerguelensis*.

thyris are found in a variety of originally soft sediments from the Pliocene and Pleistocene periods (Allan 1960; Neall 1972).

Australian Tertiary deposits consist almost exclusively of originally soft sediments. As noted above, an almost continuous Tertiary record of anakineticinids is available from the Eocene period. In addition, a number of terebratelline genera occur in sediments deposited during the Oligocene and Miocene in embayments of the southern coastline—the Otway, Gippsland and Murray basins. These genera were specialised to varying degrees for soft sediments (limestones). The only living terebratellines found in Australian waters are *Magellania flavescens* and *Jaffaia jaffaensis*.

Foster (1974) records that brachiopods similar or identical to the Recent South American species *Magellania venosa* and *Terebratella dorsata* occur in Antarctic strata of Oligocene and Miocene age. No fossil records are known of *Aerothyris*, *Aneboconcha*, *Dyscritosia*, *Syntomaria*.

All terebratelline genera, living and fossil, are endemic with the single exception of *Stethothyris sufflata*. This species, like another form (*Neobouchardia minima*) specialised for free life in carbonate sands occurs in Oligocene deposits of both Australia and New Zealand.

In general then, members of the southern subfamilies of the Terebratellidae appear to be consistent in nature and distribution and in their response to environmental changes. They occupy rocky shorelines and shelves but not the slopes (with the exception of *Magellania venosa*) or the abyss and similar forms occur in similar habitats. Species with specialist characters occur only in sediments of a specific nature (although generalists may also occur therein), e.g. greensands, bryozoan sands. As could be predicted, response to environmental change differs in generalist and specialist forms. The New Zealand record shows the sediment changes that accompanied Miocene regressions led to the extinction of all specialists for soft sediments while generalists appear to have occupied shoreline habitats since the Eocene. Members of both the Anakineticinae and Bouchardiinae are all substrate-specific forms and so are limited in distribution. The Terebratellinae are not substrate specific and are widely distributed within the Southern Hemisphere.

ORIGINS

The origins and the means of distribution of the Terebratellidae have been discussed by Thomson (1918), Blochmann (1908), von Ihering (1903) and Allan (1963). They agree that the probable source

of origin was Gondwana and that shallow seas around land bridges would have provided routes for the dispersal of ancestral forms. They came to this conclusion in view of:

1. the unlikelihood that transoceanic dispersal could occur with a non-planktotrophic larva;

2. the endemic nature of the faunas of South America, New Zealand and Australia;

3. the lack of evidence of land bridges connecting these southern lands during the Tertiary.

This view of the distribution of southern faunas has not substantially altered. Plate tectonics, of course, has provided the means of distribution without the need to postulate land bridges. It has also been shown that substrate type, in addition to the length of larval life, is a limiting factor in distribution (Richardson 1986). While the broad view of terebratellid distribution is shared with earlier workers, recent work on the subfamily Terebratellinae has made it possible to make a more educated guess as to the nature of ancestral stock.

Work on the Terebratellidae in all parts of their geographical range has shown consistency in patterns of distribution with the nature of species. Undifferentiated or generalist species may be widely distributed (with geography and substrate) and they are variable in those characters linked with the environment (differential thickening, beak characters, shape and size). Species specialised for shelf sediments are limited in distribution and are less variable morphologically, both distribution and variability being related to extent of specialisation.

It seems unlikely that the patterns of distribution of terebratellid brachiopods in earlier periods would differ appreciably from those evident throughout the Cainozoic. In other words, given the evidence available, the most valid working hypothesis is that the shorelines and shelf of Gondwana would have been occupied by generalist species and by species specialised to varying degrees for shelf life. With the break-up of the continent their survival would have been related to the extent of substrate loss or change. Differences in the requirements of generalists and specialists means that generalists are more likely to survive periods of environmental change as illustrated by the extinction of all taxa specialised for shelf sediments during a period of instability in the New Zealand Miocene.

The break-up of Gondwana together with the differential survival of species would account for the present distribution in which generalists and near-generalists occur around all Gondwana-derived land forms. The only specialists shared are 3 conspecifics (1 cancellothyrid and 2 terebratellid

species) and, since all were adapted for life in carbonate sands, it is likely that some part of the Gondwana shelf contributed to the shelves of Australia and New Zealand. All other specialists found in southern latitudes are endemics; i.e. they evolved in the area they now occupy. The derivation of species of one of the endemic genera, *Neothyris*, has been referred to by Neall (1972) and Aldridge (1991) and a detailed analysis of the direction of evolution in this genus is in preparation.

The difficulty all workers have experienced in separating the non-specialist members of the subfamily Terebratellinae is an indicator of the close relationship existing between species now attributed to *Terebratella*, *Magellania*, *Aerothyris*, *Fosteria*, *Syntomaria*, *Aneboconcha*, *Dyscritosia*, *Calloria*, *Magasella*. These similarities are the result of relatedness not of convergence because they occur in sets of characters which appear to be independent of the environment. Morphological differences are most pronounced in Australian and New Zealand species which differ from each other and from South American and Antarctic species to a greater extent than any of the latter differ from each other. Australia and New Zealand are also the most isolated land forms whereas chains of islands form shallow connections between South America and Antarctica. Morphological differences may therefore be associated with greater isolation during the Cainozoic. Differences may also have resulted from the nature of the generalist stock that occupied different parts of the Gondwana coastline. In both Australia and New Zealand populations of *Magellania flavescens*, *Calloria inconspicua* and *Magasella sanguinea* vary with either or both geography and habitat (Stewart 1975, 1981; Aldridge 1981). For example, 3 geographical variants of *Magasella sanguinea* occur on different coasts—the east coast of the North Island, the west coast of the North Island, all coasts of the South Island together with the south coast of the North Island. A hypothetical break-up of New Zealand would mean that slightly different stocks would be separated according to the lines of fracture.

DISCUSSION

Chronologically, the Terebratellidae is the youngest articulate family and comparison of its character with that of older families is of interest in view of the repetitive history of articulates (Cooper 1970; Rudwick 1970). Families of the Rhynchonelloidea and the Terebratuloidea are cosmopolitan and abyssal and members may be widely separated whereas the Terebratellidae are concentrated in

the area of their presumed origin and no taxa have been collected from bathyal or abyssal waters. The restricted distribution of the Terebratellidae throughout their history also makes it unlikely that they would have originated with all other members of the Phylum in seas at low latitudes as suggested by Zczina (1985). An origin in low latitudes would require extensive transoceanic travel which seems unlikely given the brevity of larval life and the substrate specificities of some members.

Family evolution is a field in which little conjecture has been possible because of the difficulty in older families of establishing the nature of relationships between species. Relationships in these families are masked by a combination of age, stasis, convergence and by the paucity of living members. Older families are cosmopolitan and, as a rule, their members do not occur in abundance. The Thecideoidea, Rhynchonelloidea, Cancellothyroidea, Terebratuloidea were all more common in past eras—numbers of genera in the Rhynchonelloidea, for example, declined from 113 in the Jurassic to 17 in the Recent, the Terebratuloidea from 136 to 19 in the same periods (Cooper 1988). Age, together with sparse occurrence and cosmopolitan distribution means that the present composition of these superfamilies is unrepresentative, i.e. they are remaindered groups which have shown no evidence of diversification since, at least, the Jurassic (Cooper 1988) and therefore relationships between species and genera would be impossible to determine. As a consequence, the present composition and distribution of non-terebratelloid families can provide little information on origins and paths of dispersal of articulates. The degree of specialisation of the terebratellid subfamilies Bouchardiinae and Anakinetiinae also makes any analysis of relationships difficult.

More productive ground for conjecture is provided by the Terebratellinae. Since a substantial amount of information on ecology is now available, factors other than preservable hard parts can be included in any assessment; e.g. studies of the members of this family have shown that the pedicle does not function as an anchor chain but as an appendage, that it is highly variable and that its muscles and their function determine the structures of the cardinalia. Therefore, the morphological variability of terebratelline taxa is derived from the variability in substrate relationships that characterises generalist taxa. Specialist taxa with a constant substrate relationship show lower morphological variability. Generalist and near-generalist species comprise the bulk of species attributed to the Recent Terebratellinae and they appear to have the capacity to give rise to more

specialised forms by the colonisation of substrates that are less variable than those in shoreline regimes. Evidence that endemic species specialised for shelf sediments may be derived from generalist shoreline stock living in the same area will be examined in detail in a forthcoming paper on the species of *Neothyris* and *Magasella* now living in New Zealand waters.

It is of interest to note the distribution with depth of species from different families. Members from families belonging to the Rhynehonelloidea and Terebratuloidea occur on the shorelines and/or shelves of both Australia and New Zealand and, in addition, have been collected from abyssal sediments of the Tasman Sea whereas members of the Terebratellidae are known only from the continental shelves. This pattern suggests that a correlation may exist between family age and extent of distribution with depth. It gives some support to the present supposition of the shoreline as a generative zone with direction of spread from shoreline to shelf to slope to abyss.

A pattern of distribution similar to the Terebratellidae is evident in laqueid genera from the north Pacific rim. Generalists are found around shorelines and it appears that diversification of this stock has resulted in species specialised for different shelf sediments in Japan and California, e.g. a generalist stock similar to *Terebratalia coreanica* is considered to be ancestral to the shelf species *Coptothyris grayi* (Nomura & Hatai 1936). Members of the Laqueidae are not known from northern or southern circum-polar seas, the Atlantic or from abyssal sediments. It is significant that the Terebratellidae and Laqueidae are the most localised and are also the youngest articulate families.

Integration of the information now available shows that the history and present distribution of the family can best be accounted for by the redistribution of generalist stock with the Gondwana shoreline. The differentiation of this stock for particular substrates has occurred in areas that now differ in degrees of isolation, in the range of sediments available and in tectonic stability. Determination of the character of terebratellid faunas by these variables is well illustrated from the Australian and New Zealand records. Carbonate sands and bioclastic limestones were deposited in both regions during the early to middle Tertiary and they contained large assemblages of terebratellids (anakinetioides and terebratellinids) specialised for free life. The drastic reduction of shallow marine shelf environments with plate movement during the Miocene in New Zealand resulted in their extinction whereas the greater stability of Australia and the retention of carbon-

ate sands has meant that assemblages (almost exclusively anakinetioides) in modern seas replicate those found in Tertiary deposits. The modern terebratellid fauna of New Zealand consists exclusively of members of the subfamily Terebratellinae and species of only 2 genera (*Neothyris*, *Gyrothyris*) may illustrate early stages in the process of adaptation for the terrigenous sediments that now surround New Zealand.

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